

FORAGES

The Relationship of Leaf Strength to Cattle Preference in Tall Fescue Cultivars

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ABSTRACT

Low values of leaf blade tensile and shear strength have been related to herbivore preference and intake in perennial ryegrass (*Lolium perenne* L.) and other forage grasses. This study examined relationships between leaf strength and cattle (*Bos taurus*) preference for eight cultivars of tall fescue (*Festuca arundinacea* Schreb.). Both tensile strength and shear strength of tall fescue leaf blades were measured, along with several leaf blade anatomical characteristics. Leaf tensile strength was negatively correlated ($r = -0.20$, $P \leq 0.01$) with preference in this study. 'Mozark', the cultivar with the highest leaf tensile strength, also had the highest proportion of structural tissue in leaf blade transverse sections. Shear strength was also negatively correlated with preference ($r = -0.16$, $P \leq 0.05$). Leaf strength of both chamber- and field-grown plants was negatively correlated with both leaf blade width and thickness. Leaf width and thickness increased together and were positively correlated with preference in all experiments. Wider leaves also had greater distance between veins and therefore more mesophyll tissue volume. We concluded that leaf width would be a useful trait in the selection of grasses for cattle preference, since it would result in grasses with a higher proportion of cell contents to fiber. This conclusion is supported by the positive correlation of preference with total nonstructural carbohydrates in an earlier study of the same tall fescue cultivars.

GIVEN THE OPPORTUNITY to select among forages, grazing animals respond to a combination of physical properties and chemical cues that result in preference (Beaumont et al., 1933). A factor frequently correlated with preference is tensile strength (Beaumont et al., 1933; Theron and Booysen, 1966), which is the force per cross-sectional area exerted by longitudinal pull that is required to break a leaf. Tensile strength is equated with resistance to the pulling motion cattle use when grazing. Evans (1964) determined the range of tensile strengths among varieties of perennial, Italian (*L. multiflorum* Lam.), and hybrid ryegrasses [*L. perenne* \times *L. multiflorum* and *L. perenne* \times (*L. perenne* \times *L. multiflorum*)]. The ryegrasses with higher tensile strength, which increased in proportion to perennial ryegrass content, also had a higher percentage of structural tissue. In a related study, the ryegrasses with the

lowest tensile strength were found to produce the highest animal gains (Rae et al., 1964).

Shear strength is also a breaking force per cross-sectional area, but in this case the force is applied at 90° to the longitudinal axis of the leaf. Lambs (*Ovis aries*) ate for longer periods and had higher forage intake when fed perennial ryegrass selected for leaves with lower shear strength, and the digestibility rate of this forage was also higher (Inoue et al., 1989). High shear strength has been equated with resistance to chewing, and grasses with lower shear strength should break down faster during chewing, allowing ruminants to consume more dry matter (MacKinnon et al., 1988). Perennial ryegrass selections with low shear strength were chewed less by sheep than selections with higher shear strength (Inoue et al., 1994b).

Most recently, preference in ruminants has been associated with factors that contribute to increased rate of intake. Sheep grazing smooth brome grass (*Bromus inermis* Leyss.) preferred clones with high in vitro dry matter disappearance (IVDMD) to low-IVDMD clones, and clones with low neutral detergent fiber (NDF) to high-NDF clones (Falkner and Casler, 1998).

Previous research determined that cattle prefer certain tall fescue cultivars over others (Shewmaker et al., 1997), and in a follow-up study, cattle preference for these cultivars was positively correlated with total nonstructural carbohydrate (TNC) concentration (Mayland et al., 2000). We hypothesized that cattle preference among these tall fescue cultivars would also be related to leaf strength and percentage of structural tissue, as studies with ryegrasses had found. Since leaf strength in grasses is a function of the content and distribution of fiber cells (Vincent 1982), low leaf strength implies a reduction in fiber relative to the content of thin-walled mesophyll tissue, which is highly digestible. Therefore, the negative correlation of ruminant preference with leaf strength may actually indicate a preference for grasses with a higher proportion of mesophyll tissue. Such grasses would also have high TNC concentration and digestibility, and promote higher intake and gain, all associated with preference. Our objective was to characterize leaf strength and other anatomical characteristics that could be predictive of cattle preference differences among tall fescue cultivars.

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Abbreviations: IVDMD, in vitro dry matter disappearance; NDF, neutral detergent fiber; PAR, photosynthetically active radiation; TNC, total nonstructural carbohydrates; VHO, very high output.

MATERIALS AND METHODS

Growth Chamber Plant Culture

The endophyte-free tall fescue cultivars 'Barcel', 'HiMag', 'Kentucky-31' (KY-31), 'Missouri-96' (MO 96), 'Mozark', 'Stargrazer', and the endophyte-free *Festuca/Lolium* hybrid 'Kenhy' were established from single clones of each cultivar. A pot was considered one replicate, and each pot was established with seven vegetative tillers, so a total of 42 vegetative clones of a single plant from each cultivar was used.

Tillers were established in 3.5-L pots containing Terra-Lite Redi-Earth Peat-Lite potting mix (Scotts-Sierra Horticultural Products Co., Marysville OH). During the first 12 wk of plant growth, all replicates were maintained in a single growth chamber with 15/9 h light/dark intervals and 22/17°C day/night temperatures. These temperatures are in the optimal range for tall fescue growth (Wolf et al., 1979). Light was provided by both VHO (very high output) fluorescent and incandescent sources at an intensity of 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR (photosynthetically active radiation). After this establishment period, pots from three replicates were arranged in blocks in each of two growth chambers maintained as above.

Both plant-to-plant and leaf-to-leaf variation have been high in previous studies of leaf blade tensile strength (Knee-bone, 1960), so tillers of a single clone of each cultivar were grown in growth chambers, and leaves of different cultivars were compared at the same stage of development for anatomical characteristics and tensile strength. Plants were clipped at the approximate ligule height of mature leaf blades of each cultivar at 6-wk intervals and fertilized with a solution containing the equivalent of 1 g L⁻¹ N, 0.46 g L⁻¹ P, 0.87 g L⁻¹ K, and 0.15 g L⁻¹ S. At sampling, growth chamber-grown plants were sufficiently mature that tillers filled the pot. Leaves were sampled approximately 3 wk after a clipping, when canopies had three fully expanded leaves per tiller but before the oldest leaf blades on tillers began to senesce.

Leaf Anatomy

The width of fully expanded tall fescue leaf blades increases with distance from the ligule toward the middle of the leaf and becomes constant over a limited region before beginning to taper toward the tip (MacAdam, 1988). Width of the youngest fully expanded leaf of three tillers per pot was determined at intervals from the ligule through 300 mm toward the leaf tip with an ocular micrometer, and the region where leaf blade width was both maximal and constant was determined for each cultivar. Leaf blade transverse area and fiber bundle area as a proportion of transverse area were determined at the center of this region as described below.

The upper surface of tall fescue leaf blades is ridged, making it difficult to accurately measure leaf blade thickness and calculate cross-sectional area. Major ridges contain veins with metaxylem cells, and minor ridges contain veins with no metaxylem; major and minor veins alternate across the width of the leaf (Cohen et al., 1982). To determine leaf blade cross-sectional area, 1 cm long segments centered in the region of constant leaf width were excised from the youngest fully expanded leaf blade of one tiller from each replicate, and fixed in 4 mL of 2.5% w/v glutaraldehyde in 0.1 M K-phosphate buffer, pH 7.0. Following 1 h vacuum infiltration at 50 to 65 kPa, leaf blade segments were stored in fixative overnight at 4°C, and rinsed four times for 15 min each in 4 mL of 0.1 M K-phosphate buffer, pH 7.0. Following fixation, segments were dehydrated for 30 min per solution in a 20–40–60–80–100% v/v ethanol series to clear and preserve leaf tissue. Segments were stored overnight in the first 100% ethanol solution, then rinsed two

additional times in 100% ethanol, and stored in the final rinse until microscopy was completed. Before sectioning for microscopy, leaf blade segments were rehydrated into buffer.

Transverse sections 25 μm thick were cut from leaf blade segments for microscopy with a hand microtome (Allmikro, Germany). Sections were stained with toluidine blue O for 1 min and destained for 1 min in a solution of 45% v/v EtOH, 10% v/v glacial acetic acid, and 45% v/v H₂O. Sections were mounted in buffer under a cover slip and viewed on a video monitor with a 10 \times objective and a 10 \times camera tube. The outline of a portion of the transverse section containing one major and one minor vein and their surrounding mesophyll tissue was traced on transparencies taped to the monitor screen, along with the perimeter of the abaxial and adaxial fiber bundles adjacent to each vein. The lateral margins of these tracings were fixed where the leaf was the least thick between ridges; therefore, one transverse section contained a complete pair of ridges, with one major and one minor vein.

The areas of these roughly rectangular leaf sections and of their fiber bundles were determined with Delta-T Scan (Delta-T Devices Ltd., Cambridge, UK) software calibrated to known areas. Because the upper leaf blade surface is ridged, leaf blade thickness was calculated for each traced section by dividing total transverse area by section width.

Tensile Strength: Growth Chamber-Grown Plants

Six leaves from three replicates of each cultivar were harvested from growth chamber-grown plants, wrapped in wet paper towels, and delivered overnight from Logan, UT, to the USDA-ARS Western Regional Research Laboratory in Albany, CA. Tensile breaking strength was measured at the location of maximal leaf blade width with a Texture Analyzer, TA-XT2 (Texture Technologies, Scarsdale, NY). The remaining three replicates were harvested the following day and analyzed in the same way.

Shear Strength: Field-Grown Plants

Shear strength was determined on newly mature leaf blades of the seven cultivars used for tensile strength (Barcel, HiMag, Kenhy, KY-31, MO 96, Mozark, and Stargrazer) plus the tall fescue variety 'C-1'. Cultivars were grown in an irrigated Portneuf silt loam loess soil (Durinodic Xeric Haplocalcid) near Kimberly in south-central Idaho (42°30' N, 114°08' W, elev. 1200 m) as part of a cattle preference study (Shewmaker et al., 1997). The cultivars C-1 and HiMag were selected for reduced K/(Mg + Ca) and therefore reduced risk of grass tetany in ruminants (Mayland and Sleper, 1993).

Leaf blades were clipped in the late evening of 29 June 1995, wrapped with damp paper towels, chilled to approximately 5°C, and transported to the laboratory. Shear strength was measured the following day with a QTRS-25 guillotine equipped with a square blade (Stevens Farnell Quality and Test Systems, Dunmow Essex, UK). Leaves were manually held on the slotted table while the blade passed through the leaf at a rate of 50 mm min⁻¹. Shear strength was measured at the widest part of eight mature leaf blades from each cultivar. Leaf width was determined with a dissecting 10 \times binocular scope fitted with a calibrated scale. Leaf thickness was assessed with a micrometer having 6.35 mm diam. opposing pins (Scheer-Tumico, St. James, MN) that were in contact with both sides of the leaf during measurement.

Statistical Analysis

The leaf anatomy and tensile strength experiments used clones of the same seven growth chamber-grown cultivars

Table 1. Cattle preference scores for tall fescue cultivars grazed in each of four seasons and 2 yr, where 0 represented no evidence of grazing and 10 indicated all available forage was eaten (adapted from Shewmaker et al., 1997).

Cultivar	Preference							
	1993				1994			
	May	June	Aug.	Sept.	May	June	Aug.	Sept.
Kenhy	7.1	6.4	8.6	7.7	6.8	8.8	8.6	8.2
KY-31	5.3	3.9	7.1	5.2	3.9	7.3	6.9	6.6
HiMag	4.5	4.0	7.4	4.4	3.8	6.6	6.6	6.5
C-1	6.6	3.9	5.6	5.3	4.0	5.9	5.9	5.0
Stargrazer	4.0	3.7	6.8	4.2	3.7	6.4	6.5	6.8
Barcel	4.5	3.3	6.4	4.0	2.9	6.5	6.4	6.8
MO-96	4.6	3.1	6.5	3.4	2.9	5.8	5.7	5.4
Mozark	3.9	2.4	6.1	2.9	1.9	6.3	6.4	6.8

arranged in a randomized complete block design, with six pots per cultivar serving as blocks (replicates). The shear strength field study was a randomized complete block design with eight cultivars in three blocks (replicates). The six leaves per pot in the tensile strength experiment and the eight leaves per cultivar in the shear strength experiment were considered subsamples. Analyses of variance were conducted with the ANOVA procedure of SAS (2000) and means separations were based on the LSD.

The leaf characteristics measured in the present study were related to the means of eight trials of cattle preference performed over a 2-yr period (Table 1) as reported by Shewmaker et al. (1997). In that study, the grazing preferences of cattle among seven endophyte-free cultivars of tall fescue and one tall fescue–annual ryegrass (*Lolium multiflorum* L.) hybrid were quantified. Results in descending order of preference were Kenhy > KY-31 > HiMag = C1 = Stargrazer = Barcel > MO-96 = Mozark. Correlation coefficients were determined with the CORR procedure of SAS (SAS Inst., 2000).

RESULTS AND DISCUSSION

Leaf Width Profiles

In earlier studies, grass leaf tensile strength was tested by placing leaf blades in clamps at a constant distance from the collar (Kneebone, 1960; Connor and Bailey, 1972) or by testing the middle segment of the leaf blade (Evans, 1967; Theron and Booyesen, 1968; Inoue et al., 1989, 1994a). However, leaves tended to break at the clamp (Evans, 1967) because cross-sectional area and therefore leaf strength was lower at one clamp than the other due to differences in leaf width (Kneebone, 1960; Martens and Booyesen, 1968; John et al., 1989). As illustrated for the cultivars Barcel and MO-96 (Fig. 1), the leaf blade midpoint occurs at a location where the leaf has already begun to taper toward the tip. The length of individual leaf blades of chamber-grown plants ranged from 380 to 520 mm (Table 2), which is typical for tall fescue grown in the field (Terrell, 1979).

When grazed by cattle in the field, tall fescue leaves would be most likely to break near the base of the leaf blade because they are most narrow at the ligule or the leaf tip (Fig. 1). However, a 50-mm length of leaf is required for clamp placement for leaf tensile strength measurement and leaf width changes considerably over short distances at the leaf base. As seen in Fig. 1, there is a region of constant maximal width in fully expanded

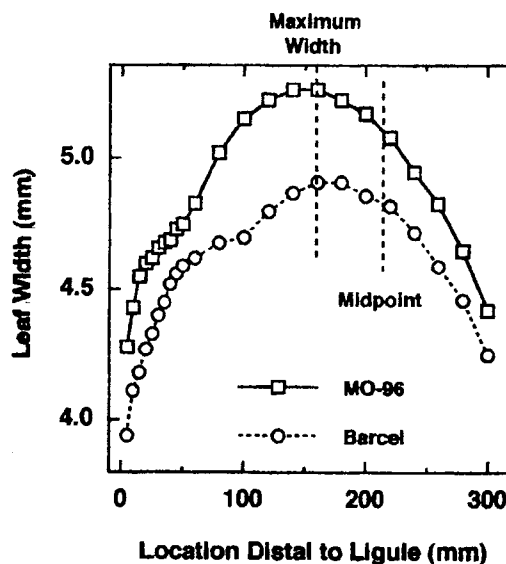


Fig. 1. Width of leaf blades of two cultivars of tall fescue from the ligule through 300 mm toward the leaf tip. Leaves continue to taper for at least another 100 mm. The location of the center of these leaf blades was approximately 215 mm distal to the ligule. Maximum width and leaf midpoint are indicated to demonstrate that leaf width increases for approximately the first one-third of the distance from the ligule toward the tip, then tapers toward the tip over the distal two-thirds of leaf blade length.

leaf blades that occurs over a 50 to 80 mm long region centered from 120 to 190 mm distal to the ligule, about one-third of the distance from the ligule to the leaf tip, and maximum width of individual leaves at this location ranged from 4.5 to 7.8 mm (Table 2).

Vein number in grass leaves will be constant where leaf width is constant, as will the number of fiber bundles, which are associated with veins (MacAdam and Nelson, 2002). Therefore, the region of constant width should provide the most reproducible data for leaf blade strength, and relative differences among cultivars should still be representative of leaf breakage under grazing. The center of this region of constant width was chosen for leaf tensile strength measurements, and as the site for further anatomical analysis of leaf blades. The above characteristics were not analyzed statistically because leaf widths and lengths were measured solely to establish the locations for analysis of other leaf characteristics.

Leaf Anatomy: Growth Chamber-Grown Plants

Transverse leaf blade sections from the region of constant width were examined by light microscopy to determine mean leaf blade thickness and proportion of structural tissue in transverse area. Cultivars with the highest preference (Table 1) also had the thickest leaf blades (Table 2); KY-31 was 24% thicker than MO-96. The cultivars with thickest leaves also had the greatest transverse areas.

A higher content of thin-walled mesophyll cells, which are rapidly and completely digested in cool-season grasses such as tall fescue (Akin, 1989), would result in greater leaf blade concentrations of soluble nutrients

Table 2. Mean leaf blade length and location of the region of maximum width with respect to the ligule of the youngest fully mature leaf blade of one tiller per pot of growth chamber-grown tall fescue cultivars. Other characteristics measured at location of maximum leaf width were leaf blade thickness, the width and transverse area of a representative pair of ridges, and the proportion of transverse leaf area occupied by fiber cell bundles.

Cultivar	Leaf blade length	Maximum leaf blade width	Location of maximum width		Leaf blade thickness	Two ridges		Fiber cell bundle, % transverse area
			Distance from ligule	% of leaf length		Width	Area	
		mm		%	mm		mm ²	%
Kenhy	454	7.3	138	30	0.25 ab†	0.88 a	0.219 a	1.02 bc
KY-31	416	7.0	138	33	0.26 a	0.84 a	0.222 a	1.16 abc
Hi-Mag	463	6.5	160	35	0.25 ab	0.82 ab	0.205 ab	0.53 c
Stargrazer	405	6.3	162	40	0.22 bc	0.73 b	0.161 c	0.63 bc
Barcel	447	4.7	150	34	0.22 bc	0.74 b	0.164 c	1.46 abc
MO-96	414	5.1	153	37	0.21 c	0.74 b	0.152 c	1.56 ab
Mozark	487	5.1	162	33	0.22 bc	0.80 ab	0.173 bc	2.13 a
SE					0.005	0.014	0.0068	0.144

† Values in a column followed by the same letter are not different at $P \leq 0.05$.

such as carbohydrates, proteins, and lipids, which are readily available to ruminants. In an earlier study of the same tall fescue cultivars (Mayland et al., 2000) leaf blade concentration of total nonstructural carbohydrates was positively correlated with preference ($r^2 = 0.49$; $P < 0.05$).

The width of two adjacent ridges was greatest in the most preferred cultivars, Kenhy and KY-31 (Table 2). Since we were evaluating sections containing two veins in each case, cultivars with greater width would also have a higher proportion of mesophyll tissue and therefore higher cell contents, giving those cultivars greater digestibility and intake potential. The higher intake and digestibility of C_3 compared with C_4 grasses is attributed to the wider spacing of veins and resulting higher proportion of leaf blade transverse area occupied by mesophyll (photosynthetic) tissue compared with vascular and structural tissues in C_3 grasses (Akin, 1989).

The maximum leaf blade width data reported in Table 2 are the means of 18 observations that were repeated at intervals along leaves to determine the location of maximum leaf width, whereas the leaf width data in Table 3 are the means of 36 observations for leaves from the same growth chamber-grown plants made at the location of maximum leaf blade width when tensile strength data were taken. While the width data are not identical, the ordering of varieties from least to greatest width is consistent for the two experiments. Leaf blade thickness data in Table 2 were derived from six observations of the transverse area of two ridges per leaf determined at a magnification of 100 \times , and therefore is less

than leaf blade thickness measured directly with a micrometer (Table 3) that could only determine maximum thickness. However, as with leaf width, the order of leaf blade thickness data for varieties is consistent for the two experiments. Leaf blade width and thickness increased together in whole leaves in the tensile strength (Table 3) and shear strength (Table 4) experiments. Increases in leaf width, thickness, and transverse area were negatively correlated with both tensile strength and shear strength (Table 5).

Tensile Strength: Growth Chamber-Grown Plants

Tensile breaking strength is measured as force in Newtons (N) mm⁻² of transverse leaf blade area. Tensile strength differed among tall fescue cultivars (Table 3), and was negatively correlated with preference (Table 5). In grass leaves, fiber cells are found either located above and below veins where they are grouped in fiber bundles with a relatively large transverse area per bundle or as a ring of single fiber cells encircling veins in bundle sheaths. In leaf blades of perennial ryegrass, fiber bundles were the primary contributors to tensile strength (Vincent, 1982). A tensile strength of 22 600 N mm⁻² was recorded for fiber bundles, compared with 838 N mm⁻² for vascular bundles in the same leaves. Vascular bundles include many thin-walled (phloem and parenchyma) cells in addition to xylem elements and the ring of fiber cells (inner bundle sheath). Whole grass leaves are composed of longitudinally oriented veins and fiber bundles interspersed with groups of thin-walled mesophyll cells, and covered with sheets of epidermal cells.

Table 3. Mean tensile strength and transverse section dimensions of mature leaf blades of growth chamber-grown tall fescue after 3 wk of regrowth.

Cultivar	Width	Thickness	Transverse area	Tensile strength
	mm	mm	cm ²	N mm ⁻² †
Kenhy	8.2 a†	0.38 b	3.1 b	7.21 c
KY-31	7.8 b	0.45 a	3.6 a	8.10 b
HiMag	6.4 d	0.36 b	2.3 c	6.20 d
Stargrazer	7.0 c	0.37 b	2.6 c	7.65 bc
Barcel	5.4 e	0.31 c	1.7 d	8.88 a
MO-96	5.5 e	0.32 c	1.8 d	7.13 c
Mozark	5.3 e	0.33 c	1.8 d	9.51 a
SE	0.09	0.004	0.06	0.121

† Values in a column followed by letters in common are not different at $P \leq 0.05$.

‡ Newtons mm⁻².

Table 4. Mean shear strength and transverse section dimensions of mature leaf blades of field-grown tall fescue cultivars.

Cultivar	Width	Thickness	Transverse area	Shear strength
	mm	mm	mm ²	g mm ⁻²
Kenhy	9.0 a†	0.45 b	4.1 ab	833 bc
KY-31	8.8 ab	0.49 a	4.3 a	807 c
HiMag	8.0 cd	0.39 cd	3.1 d	888 abc
C-1	7.7 de	0.41 bc	3.2 cd	897 abc
Stargrazer	8.6 ab	0.42 bc	3.7 bc	938 a
Barcel	7.3 e	0.38 d	2.8 d	921 ab
MO-96	7.7 de	0.41 bc	3.2 cd	907 ab
Mozark	8.4 bc	0.44 b	3.7 bc	921 ab
SE	0.10	0.005	0.08	13.2

† Column values followed by a letter in common are not different at $P \leq 0.05$.

Table 5. Pearson correlation coefficients among leaf characteristics of tall fescue cultivars. Data for leaf dimensions are from Table 2, data for tensile strength are from Table 3, and data for shear strength are from Table 4. Cattle preference data are from Shewmaker et al. (1997) as presented in Table 1.

Leaf dimensions	Leaf thickness	Adjacent ridge transverse area	Structural area, %	Cattle preference
Adjacent ridge width	0.51***	0.02 NS†	0.12 NS	0.46**
Leaf thickness		0.17 NS	0.02 NS	0.35*
Adjacent ridge transverse area			-0.24 NS	0.25 NS
Structural area, %				-0.24 NS
Tensile strength	Leaf thickness	Leaf transverse area	Tensile strength	Cattle preference
Leaf width	0.75***	0.92***	-0.33***	0.66***
Leaf thickness		0.93***	-0.29***	0.33***
Leaf transverse area			-0.30***	0.52***
Tensile strength				-0.20**
Shear strength	Leaf thickness	Leaf transverse area	Shear strength	Cattle preference
Leaf width	0.70***	0.92***	-0.50***	0.25**
Leaf thickness		0.92***	-0.51***	0.17*
Leaf transverse area			-0.55***	0.24***
Shear strength				-0.16*

* Significant at $P < 0.05$.

** Significant at $P < 0.01$.

*** Significant at $P < 0.001$.

† NS, not significant at $P < 0.05$.

Therefore, change in the cross-sectional area of groups of fiber cells in fiber bundles will significantly affect leaf strength. By comparison with our data for tensile strength (Table 3), Vincent's (1982) values for tensile strength are high, but that is because his measurements are for isolated fiber bundles or vascular bundles while ours are for whole leaves. Mozark, the tall fescue cultivar with the highest tensile strength, also had the highest proportion of fiber bundle transverse area (Table 2).

Shear Strength: Field-Grown Plants

Differences among shear strengths of field-grown cultivars of tall fescue were small, decreasing by only 14% from highest to lowest (Table 4). As with tensile strength, shear strength was negatively correlated with preference (Table 5), and the two lowest shear strength cultivars, Kenhy and KY-31, were also the most preferred (Table 1). Since high shear strength indicates greater resistance to leaf breakdown through chewing, low shear strength may be associated with cattle preference because more rapid liberation of cell contents would be consistent with increased forage nutritive value (e.g., Mayland et al., 2000).

In Grasslands 'Nui' perennial ryegrass the cross-sectional area of abaxial fiber bundles was 67% lower in low shear-strength selections than in high-strength selections (Inoue et al., 1994a). This suggests that low shear strength reflects either a decrease in structural (fiber bundle) tissue or an increase in the mesophyll tissue that occurs between veins. In the low-strength selection, fiber bundles were found only in ridges containing major vascular bundles; however, they were found in all ridges of the leaf blade in the high-strength selection.

CONCLUSIONS

Leaf strength of both field-grown and growth chamber-grown tall fescue cultivars was negatively correlated

with preference. Tensile strength is related to resistance to initial leaf breakage by grazing, and fiber bundles are the primary source of leaf strength. The cultivar with the highest proportion of fiber bundle area also had the highest tensile strength. Leaves with low shear strength would break down most easily with chewing and therefore would provide access to leaf nutrients most readily. The cultivars with the lowest shear strengths were also the most preferred. The leaf characteristic most associated with preference across experiments was leaf width. Greater width between veins and associated increase in thickness indicates a higher ratio of mesophyll to structural tissue and therefore potentially higher cell contents availability and higher nutritive value. Leaf blade width and thickness increased together and both were positively correlated with cattle preference, particularly when maximum width was measured. Therefore, maximum leaf blade width would be a practical and convenient trait to use in breeding for increased grazing preference in grasses.

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REFERENCES

- Akin, D.E. 1989. Histological and physical factors affecting digestibility of forages. *Agron. J.* 81:17-25.
- Beaumont, A.B., R.E. Stitt, and R.S. Snell. 1933. Some factors affecting the palatability of pasture plants. *J. Am. Soc. Agron.* 25:123-128.
- Cohen, C.J., D.O. Chilcote, and R.V. Frakes. 1982. Leaf anatomy and stomatal characteristics of four tall fescue selections differing in forage yield. *Crop Sci.* 22:704-708.
- Connor, H.E., and R.W. Bailey. 1972. Leaf strength in four species of *Chionochloa* (*Arundineae*). *N.Z. J. Bot.* 10:515-532.
- Evans, P.S. 1964. A study of leaf strength in four ryegrass varieties. *N.Z. J. Agric. Res.* 7:508-513.
- Evans, P.S. 1967. Leaf strength studies of pasture grasses: I. Apparatus,

- techniques and some factors affecting leaf strength. *J. Agric. Sci. (Cambridge)* 69:171-174.
- Falkner, L.K., and M.D. Casler. 1998. Preference for smooth brome-grass clones is affected by divergent selection for nutritive value. *Crop Sci.* 38:690-695.
- Inoue, T., I.M. Brookes, T.N. Barry, and A. John. 1989. Effects of selection for shear strength on the voluntary intake and digestion of perennial ryegrass fed to sheep. *Proc. N.Z. Soc. Anim. Prod.* 49:221-224.
- Inoue, T., I.M. Brookes, A. John, F.W. Hunt, and T.N. Barry. 1994a. Effects of leaf shear breaking load on the feeding value of perennial ryegrass (*Lolium perenne*) for sheep: I. Effects on leaf anatomy and morphology. *J. Agric. Sci. (Cambridge)* 123:129-136.
- Inoue, T., I.M. Brookes, A. John, E.S. Kover, and T.N. Barry. 1994b. Effects of leaf shear breaking load on the feeding value of perennial ryegrass (*Lolium perenne*) for sheep: II. Effects on feed intake, particle breakdown, rumen digesta outflow and animal performance. *J. Agric. Sci. (Cambridge)* 123:137-147.
- John, A., T. Inoue, I.M. Brookes, W.F. Hunt, and H.S. Easton. 1989. Effects of selection for shear strength on structure and rumen digestion of perennial ryegrass. *Proc. N.Z. Soc. Anim. Prod.* 49:225-228.
- Kneebone, W.R. 1960. Tensile strength variations in leaves of weeping lovegrass [*Eragrostis curvula* (Schröd.) Nees.] and certain other grasses. *Agron. J.* 52:539-542.
- MacAdam, J.W. 1988. Cellular dynamics, peroxidase activity, and secondary cell wall deposition during tall fescue leaf blade development. Ph.D. diss. Univ. of Missouri, Columbia (Diss. Abstr. 89-04443).
- MacAdam, J.W., and C.J. Nelson. 2002. Secondary cell wall deposition causes radial growth of fibre cells in the maturation zone of elongating tall fescue leaf blades. *Ann. Bot.* 89:89-96.
- Mackinnon, B.W., H.S. Easton, T.N. Barry, and J.R. Sedcole. 1988. The effect of reduced leaf shear strength on the nutritive value of perennial ryegrass. *J. Agric. Sci. (Cambridge)* 111:469-474.
- Martens, P.O., and P. de V. Booysen. 1968. A tensilemeter for the measurement of the tensile strength of grass leaf blades. *Proc. Grassl. Soc. So. Afr.* 3:51-56.
- Mayland, H.F., G.E. Shewmaker, P.A. Harrison, and N.J. Chatterton. 2000. Nonstructural carbohydrates in tall fescue cultivars: Relationship to animal preference. *Agron. J.* 92:1203-1206.
- Mayland, H.F., and D.A. Sleper. 1993. Developing a tall fescue for reduced grass tetany risk. p. 1095-1096. *In* M.J. Baker et al. (ed.) *Proc. Int. Grassl. Congr.*, 17th, Palmerston North, Hamilton, and Lincoln, New Zealand, and Rockhampton, QLD, Australia. 8-21 Feb. 1993. N.Z. Grassl. Assoc., Trop. Grassl. Soc. Aust., N.Z. Soc. Anim. Prod., Aust. Soc. Anim. Prod.-QLD Branch, and N.Z. Inst. Agric. Sci.
- Rae, A.L., R.W. Brougham, and R.A. Barton. 1964. A note on live-weight gains of sheep grazing different ryegrass pastures. *N.Z. J. Agric. Res.* 7:491-495.
- SAS Institute. 2000. SAS language and procedure: Usage. Version 8. 1st ed. SAS Inst., Cary, NC.
- Shewmaker, G.E., H.F. Mayland, and S.B. Hansen. 1997. Cattle grazing preference among eight endophyte-free tall fescue cultivars. *Agron. J.* 89:695-701.
- Terrell, E.E. 1979. Taxonomy, morphology, and phylogeny. p. 31-39. *In* R.D. Buckner and L.P. Bush (ed.) *Tall fescue*. ASA, CSSA, and SSSA, Madison, WI.
- Theron, E.P., and P. de V. Booysen. 1966. Palatability in grasses. *Proc. Grassl. Soc. So. Afr.* 1:111-120.
- Theron, E.P., and P. de V. Booysen. 1968. The tensile properties of ten indigenous grasses. *Proc. Grassl. Soc. So. Afr.* 3:57-61.
- Vincent, J.F.V. 1982. The mechanical design of grass. *J. Mater. Sci.* 17:856-860.
- Wolf, D.D., R.H. Brown, and R.E. Blaser. 1979. Physiology of growth and development. p. 75-92. *In* R.D. Buckner and L.P. Bush (ed.) *Tall fescue*. ASA, CSSA, and SSSA, Madison, WI.